Field Crops Research 224 (2018) 67–75

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Assessing different barley growth habits under Egyptian conditions for enhancing resilience to climate change

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ARTICLE INFO

Keywords:
Climate change
Resilient genotypes
Barley growth habits
Vernalization genes
Photoperiod response genes
Mediterranean region

ABSTRACT

Climate change poses challenges to agricultural production in general and to plant breeders in particular. Adaptation of cereals to the new conditions and increasingly variable situations arising from this process is essential to reduce risks and limit potential threats associated with climate hazards. This study presents the first attempt to assess the response and resilience of barley genotypes, with different growth habits across Egypt. For this purpose, eight field trials were conducted from 2013 to 2016 at three experimental sites with different winter climate configurations. The trials were sown at the end of November, following recommendations for the region. Fourteen barley genotypes were evaluated, comprising seven commercial Egyptian cultivars and seven European genotypes. The European genotypes were selected from successful cultivars from Spain, encompassing a range of growth types: two spring, three intermediate and two winter types. The cultivars were genotyped for six major adaptation genes, *Vrn-H1-2-3*, *Ppd-H1-2* and *HvCEN*. One interesting finding is that, while the Egyptian cultivars were assumed to be of spring growth type, our results demonstrate that two cultivars, namely Giza123 and Giza126, are actually intermediate types (needing just a short period of vernalization). They contain the winter allele at *Vrn-H2* together with *Vrn-H1-4,* the same as the European genotypes Cierzo and Orria, they also have an active allele at *PpdH2,* such as Hispanic. Overall, these four genotypes showed very good performance in all trials with low genotype-by-environment interaction. Moreover, a foreign late spring genotype (Pewter) was highly productive and a winter genotype (Hispanic) flowered as early as some intermediate and spring genotypes with a yield similar to genotypes currently grown in Egypt. A possible explanation for this surprising occurrence, the influence of an active allele at *PpdH2* in winter cultivars, is discussed. In relation to low temperature, a high frequency of cold nights during wintertime was observed at all experimental sites, which seemed sufficient to promote timely flowering for intermediate genotypes, although this was inadequate for promoting flowering and achieving good productivity in strictly winter genotypes (e.g. Barberousse). Our findings also highlight the potential of exotic germplasm for breeding better and more resilient cultivars for autumn and for achieving good yield levels in regions with warm winters like Egypt. The results also provide insights into the usefulness of genetic variation in growth habit for breeders seeking adaptation to climate change conditions.

1. Introduction

Climate change is producing shifts in mean values of features such as temperature and precipitation, but also increased climatic variation which is challenging agricultural production. Plant breeders must respond in creative ways, one of them being the exploration of alternative germplasm outside of the dominant types in each region. Temperature is one of the key environmental factors controlling flowering time of winter cereals (e.g. wheat and barley) (Bratzel and Turck, 2015; Laurie et al., 1995; Sharma et al., 2017; Tian et al., 2015; Trevaskis et al., 2003). Vernalization, a period of cold temperatures, is required in winter varieties to stop vegetative growth and reach flowering in time to attain good yields (Deng et al., 2015). Furthermore, vernalization is considered a critical trait due to its association with winter hardiness,

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https://doi.org/10.1016/j.fcr.2018.04.016
Received 21 October 2017; Received in revised form 12 March 2018; Accepted 27 April 2018
Available online 24 May 2018
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i.e., the capacity for surviving and avoiding damage caused by winter frosts (Cuesta-Marcos et al., 2015; Gorash et al., 2017; Hayes et al., 1997; Saisho et al., 2011).

According to growth habit, barley genotypes are generally classified into three different types: winter, spring and facultative genotypes. Growth habit is controlled mainly by allelic variation at the vernalization genes, *Vrn-H1*, *Vrn-H2* and *Vrn-H3* (von Zitzewitz et al., 2005; Saisho et al., 2011). Numerous studies have described the functional polymorphisms of *Vrn-H1* alleles (Cockram et al., 2007; Fu et al., 2005; Hemming et al., 2009; Szűcs et al., 2007; von Zitzewitz et al., 2005). These studies identified ten alleles. The winter *vrn-H1* allele has a full-length intron 1, whereas the other alleles contain insertions or different deletions in the first intron. The insertion, *Vrn-H1-7*, and deletions, *Vrn-H1-1*, *2*, *3*, *4*, *5*, *6*, *8*, *9* and *10*, were associated with partial or full reduction in vernalization requirement (Hemming et al., 2009).

Winter barley carries recessive *vrn-H1* and *vrn-H3* alleles and a dominant *Vrn-H2* (presence of the gene). Winter genotypes are tolerant to low temperatures, require a long vernalization period, and are usually sensitive to photoperiod. In general, winter types require low temperatures (0–10C) for periods of 12–60 days (Evans et al., 1975; Trione and Metzger, 1970). Nonetheless, the vernalization requirement can be supplemented by the action of additional genes, particularly when vernalization conditions are not optimum. This has been reported to occur when the photoperiod-responsive allele of gene *Ppd-H2* is present in winter varieties, accelerating the transition to reproductive stage (Casao et al., 2011a; Dubcovsky et al., 2006). Spring barley carries dominant *Vrn-H1* and recessive *vrn-H2* (Takahashi and Yasuda, 1971). Spring genotypes usually present minimal tolerance to low temperature, less sensitivity to long photoperiods and no vernalization requirement (Karsai et al., 2001; von Zitzewitz et al., 2005). This type is predominant in North Africa, Ethiopia and Southwest Asia (Saisho et al., 2011). Facultative genotypes could be considered as a subclass of winter types, exhibiting tolerance to low temperature and a very limited vernalization requirement (Karsai et al., 2001; von Zitzewitz et al., 2005), due to the combination of recessive alleles at *vrn-H1* (winter) and *vrn-H2* (absence) (Karsai et al., 2005). Given the large variability existing among winter varieties (Saisho et al., 2011; Takahashi and Yasuda, 1971), some authors (Casao et al., 2011a) proposed further differentiation of types by coining the denomination of “intermediate” for varieties with reduced vernalization need. The varieties with alleles *Vrn-H1-4* and *Vrn-H1-6* require a vernalization period clearly shorter than that needed by other winter types (Casao et al., 2011a), but still longer than required by facultative type (Hemming et al., 2009; Szűcs et al., 2007; von Zitzewitz et al., 2005). Intermediate genotypes were highly prevalent among landraces developed in autumn-sowing areas in the Mediterranean basin, such as Southern Spain, regions with warm winters (Casao et al., 2011b; Yahiaoui et al., 2008).

The genes of vernalization, photoperiod-response and earliness per se (*Eam* or *Eps* genes) play very important roles in barley adaptation. Francia et al. (2011) reported that, in the Nure × Tremois (winter × spring) population, adaptation to Mediterranean environments was driven by the allelic constitution at three major genes, *Vrn-H1*, *Ppd-H2* and *Eam6*, whose candidate gene is *HvCEN* (Comadran et al., 2012). They reported that the three genes together explained almost half of the genotypic variation (47.2% sum of squares) and more than a quarter (26.3%) of genotype × environment (GE) interaction.

Egypt extends between 22°N and 31.5°N and 25°E and 35°E, with an overall area of approximately 1×10^6 km^2. The agricultural area, though not very large (3.7 Mha), is concentrated in the northern part of the country and along the Nile river valley in a long North-South axis (Hereher, 2013). This geographical domain is characterized by mild and rainy winters, as well as hot and dry summers. The annual average minimum and maximum temperatures are 15.8 °C and 24.6 °C, respectively. While summer maximum temperatures commonly exceed 30 °C, winter minimum temperatures infrequently fall below 10 °C (Fig. 1). Extreme temperatures and high evapotranspiration in spring, together with low and variable precipitations, necessitate the use of irrigation in over 97% of agricultural land (Karajeh et al., 2013). Recently, a range of studies have described climate variability at various spatial and temporal scales across Egypt, reporting a strong intra-decadal variability of winter minimum temperature (Domroes and El Tantawi, 2005; Donat et al., 2014; El Kenawy et al., 2009; Hasanean, 2004; Hasanean and Basset, 2006). These low winter temperatures may constrain the growth of spring genotypes during wintertime. As such, it is sensible to question whether the spring type is the optimum growth habit for Egypt, in particular, and for other Mediterranean areas with similar climatic conditions, in general. Another relevant question is whether other growth types, such as winter with low vernalization requirements (intermediate type), could also be well suited under current climatic conditions in Egypt.

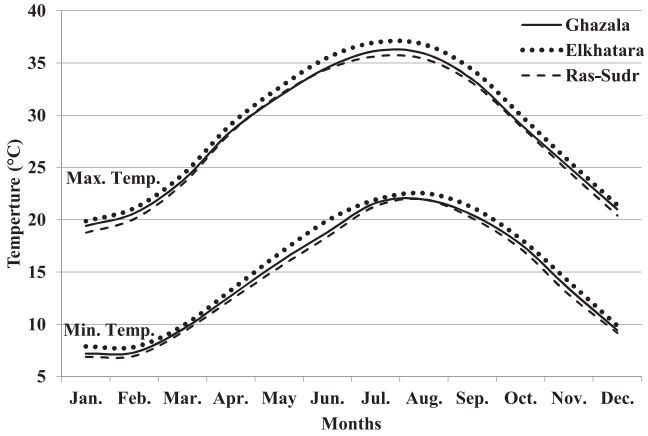

Fig. 1. Monthly averages of minimum and maximum temperatures in the three selected observatories, averaged over the period 1983–2016.

The main objectives of this study are two-fold. Firstly, to assess the agronomic performance of a range of selected spring, winter and intermediate barley genotypes under different climatic conditions across Egypt. Secondly, to evaluate whether intermediate and winter types could meet their vernalization requirements under current climatic conditions within the Egyptian context. To our knowledge, this study presents the first attempt to tackle these questions in Egypt.

2. Materials and methods

2.1. Plant material

In this study, we employed fourteen barley genotypes representing three different growth habits: winter, intermediate and spring (Table 1). Among these types, seven are supposedly spring cultivars from the Egyptian list of recommended cultivars. Due to the lack of local germplasm for winter and intermediate types, we included seven genotypes (winter, intermediate and spring) successfully cultivated in Spain.

2.2. Field trials

Eight field trials were conducted at three locations during the growing seasons in the period 2013–2016. Two sites, namely Elkhatara (Kh) and Ghazala (Gh), were located at experimental farms belonging to the Faculty of Agriculture, Zagazig University. The third site (Ras-Sudr) was located in Southern Sinai and was managed by the Desert Research Center (Table 2). These three sites represent different environmental conditions, particularly in terms of climate and soil types (Tables S1, S2). At Ghazala, soil is roughly clay (48% clay), while it is mostly sandy at Ras-Sudr (86% sand) and Elkhatara (94% sand). Moreover, Ras-Sudr is largely affected by salinity (Table S1), originating from both irrigation (4500 ppm) and the soil (5535 ppm). The

Table 1
Characteristics of the barley genotypes tested in this study (recessive alleles highlighted to enhance visibility). Allelic information is provided according to codes described in the references listed in the footnote.

Genotype	Spike type	Origin	Year of release	Growth habit	*Vrn-H1*[a]	*Vrn-H2*[b]	*Vrn-H3*[c]	*Ppd-H1*[d]	*PPD-H2*[e]	*HvCEN*[f]
Giza 123	6-rowed	Egypt	1988	Intermediate	***Vrn-H1-4***	*Vrn-H2*	*TC*	*Ppd-H1*	*Ppd-H2*	II
Giza 126	6-rowed	Egypt	1995	Intermediate	***Vrn-H1-4***	*Vrn-H2*	*TC*	*Ppd-H1*	*Ppd-H2*	II
Giza 127	2-rowed	Egypt	1995	Spring	*Vrn-H1-4*	***vrn-H2***	*TC*	*Ppd-H1*	*Ppd-H2*	III
Giza 128	2-rowed	Egypt	1995	Spring	*Vrn-H1-3*	*Vrn-H2*	*TG*	*Ppd-H1*	*Ppd-H2*	II
Giza 2000	6-rowed	Egypt	2000	Spring	*Vrn-H1-2*	*Vrn-H2*	*TG*	*Ppd-H1*	*Ppd-H2*	II
Giza 132	6-rowed	ICARDA	2006	Spring	*Vrn-H1-?*	*Vrn-H2*	*TC*	*Ppd-H1*	*Ppd-H2*	II
Giza 133	6-rowed	ICARDA	2011	Spring	*Vrn-H1-?*	*Vrn-H2*	*TC*	*Ppd-H1*	*Ppd-H2*	II
Barberousse	6-rowed	France	1977	Winter	***vrn-H1***	*Vrn-H2*	*TC*	*Ppd-H1*	***ppd-H2***	II
Cierzo	6-rowed	Spain	2004	Intermediate	***Vrn-H1-4***	*Vrn-H2*	*TC*	*Ppd-H1*	***ppd-H2***	I
Graphic	2-rowed	UK	1992	Spring	*Vrn-H1-1*	***vrn-H2***	*TC*	***ppd-H1***	*Ppd-H2*	III
Hispanic	2-rowed	France	1993	Winter	***vrn-H1***	*Vrn-H2*	*AG*	*Ppd-H1*	*Ppd-H2*	II
Orria	6-rowed	Spain	1993	Intermediate	***Vrn-H1-4***	*Vrn-H2*	*TC*	***ppd-H1***	***ppd-H2***	I
Tardana	6-rowed	Spain	2004	Intermediate	***Vrn-H1-4***	*Vrn-H2*	*TC*	*Ppd-H1*	***ppd-H2***	I
Pewter	2-rowed	UK	2001	Spring	*Vrn-H1-2*	***vrn-H2***	*TC*	***ppd-H1***	*Ppd-H2*	III

[a] Following the denominations of Hemming et al. (2009); allele coded as Vrn-H1-? indicates that it was a spring allele, different from the ones described Hemming et al. (2009), although the results did not allow a definitive allele call.
[b] Presence (dominant)/absence (recessive), as in Karsai et al. (2005).
[c] According to polymorphisms in the first intron; coded as in Casas et al. (2011), TC "early", AG "late", TG intragenic recombination.
[d] Alleles identified following Turner et al. (2005), dominant = G, recessive = T.
[e] Presence (dominant)/absence (recessive), as in Faure et al. (2007).
[f] Haplotypes following Comadran et al. (2012), I = CG, II = TC, III = TG.

experimental design with all environments was randomized complete blocks, with three replications. Individual plots consisted of six rows, 4 m long, and 20 cm spacing between rows. The plots were irrigated according to the standard practice for each location, using surface irrigation at Ghazala (250 mm in total for the entire season) and Ras-Sudr (450 mm), while Elkhatara (400 mm) was sprinkler irrigated. Application of nitrogen, potassium and phosphate fertilizers and pest, disease and weed control were carried out following the recommended agronomic practices for each region.

2.3. Climatic data

Daily minimum and maximum temperatures of three meteorological observatories, maintained by the Egyptian Meteorological Authority (*EMA*), were recorded for the last 34 years (1983–2016). These observatories were chosen based on their proximity to the experimental sites (Table 3), all being located within a maximum distance of 10 km. The selected observatories had complete records, with almost no missing values or gaps covering the whole period. To ensure the quality of the climatic data, the original dataset was tested for quality and homogeneity. This procedure aimed at identifying anomalous and suspicious data in the observatories and accordingly minimizing uncertainty related to the dataset itself (Eischeid et al., 2000; Reek et al., 1992). A detailed description of this procedure was reported by El Kenawy et al. (2013).

Here, we employed daily minimum temperature to assess changes in the frequency and magnitude of cold nights for the three meteorological observatories. For each month during an extended winter (December, January, February and March), cold nights, defined by a minimum temperature below 10C, were counted (Table S2). We believe that this figure is a good proxy for vernalization potential at each site, given that vernalization of barley reaches its peak at around 9 °C and loses effectiveness at up to 12 °C (Trione and Metzger, 1970).

2.4. Traits

The traits recorded were days to heading, days to maturity, plant height, number of spikes per square meter, number of grains per spike, thousand-grain weight, grain yield and above-ground dry matter. Days to heading represented the number of days between sowing and the date when approximately 2 cm of awns were visible on 50% of stems in the plot. Days to maturity represented the number of days between sowing and the day when approximately 50% of the spikes had ripened (turned to yellow). The grain filling period was computed as the difference between days to heading and days to maturity. Plant height was the distance in centimetres from soil surface to the top of the spike, excluding awns. The number of spikes in 0.5 m^2 was counted at maturity at two representative spots in each plot. The number of grains per spike was recorded from ten randomly chosen spikes at each plot. Both grain yield and above-ground dry matter were measured by harvesting four central rows from each plot and converting the weight to kilograms per hectare, based on the plot area that was harvested. Thousand-grain weight was determined as the weight of 1000 grains sampled from the harvest of four central rows.

Table 2
Locations, names, codes and main characteristics of the field trials.

Location	Growing season	Code	Sowing date	Latitude (N)	Longitude (E)
Ghazala	2013–2014	Gh14	27/11/2013	30.6	31.6
Ghazala	2014–2015	Gh15	12/11/2014	30.6	31.6
Ghazala	2015–2016	Gh16	19/11/2015	30.6	31.6
Elkhatara	2013–2014	Kh14	22/11/2013	30.6	32.3
Elkhatara	2014–2015	Kh15	15/11/2014	30.6	32.3
Elkhatara	2015–2016	Kh16	15/11/2015	30.6	32.3
Ras-Sudr	2014–2015	Sudr15	28/11/2014	29.6	32.7
Ras-Sudr	2015–2016	Sudr16	11/11/2015	29.6	32.7

Table 3
Locations, geographic characteristics and distance to field trials of the meteorological observatories used to characterize the climate of the testing locations.

ID	Latitude (N)	Longitude (E)	Altitude (m)	Tmin (C)*	Tmax (C)*	Tmean (C)*	Distance (km)†
Zagazig	30.6°	31.5°	17.0	14.7	28.3	21.5	10 (Ghazala)
Ismailia	30.6°	32.2°	11.0	15.3	29.0	22.1	7 (Elkhatara)
Ras-Sudr	29.6°	32.7°	16.0	14.3	27.9	21.1	3 (Ras-Sudr)

* Year average calculated using daily values for the period 1983–2016.
† Distance in km to the experimental site.

2.5. Genotyping

The genetic constitution for the vernalization and photoperiod genes of the European genotypes used in this study was known in some cases, such as Orria and Cierzo (Mansour et al., 2014) and Hispanic (Casao et al., 2011b), but it was unknown for the remaining cultivars, including all Egyptian ones. Accordingly, genomic DNA was extracted from individual leaf samples of the seven Egyptian cultivars, Barberousse, Graphic, Tardana and Pewter using the NucleoSpin Plant II kit (Macherey-Nagel, Germany). Gene-specific marker assays were performed for the different genes. *VrnH1* was scored according to the size of the first intron of its candidate *HvBM5A* (von Zitzewitz et al., 2005; Yan et al., 2003) and the alleles coded as in Hemming et al. (2009). *VrnH2* was evaluated as the presence of *HvZCCT-Ha* and *HvZCCT-Hb* (Karsai et al., 2005). *Vrn-H3* was assayed for the two polymorphisms described by Yan et al. (2006) in the first intron, then codified as in Casas et al. (2011). *PpdH1* was genotyped using SNP22 in the CCT (Constans, Constans-like, TOC1) domain of its candidate gene *HvPRR7* gene after digestion with BstU I (Turner et al., 2005). *Ppd-H2* was tested, analysing the presence/absence of the gene as previously reported (Faure et al., 2007; Casao et al., 2011a). Two SNPs in *HvCEN* were genotyped using specific KASPar markers (LGC Genomics LLC, UK). SNP positions refer to the Morex HvCEN JX648191 nucleotide sequence; intron2_T853C Primer_AlleleFAM GAGCAATCAAAAGCCTA ACGACC, Primer_AlleleHEX CGAGCAATCAAAAGCCTAACGACT, Primer_Common YCATGTTGTGCTGAGCTTATTGGTCTT; exon4_C1320G Primer_AlleleFAM AGTCCCTGGTGGAGGGAGG, Primer_AlleleHEX AGTCCCTGGTGGAGGGAGC, Primer_Common CAGAAGAAGCGGCAG GCCATGAA. The resulting haplotypes were coded according to Comadran et al. (2012).

2.6. Statistical analysis

A combined analysis of variance for each trait was performed, considering genotype, location and year as fixed factors. The analysis was performed using the unbalanced analysis of variance procedure provided in GenStat (version 18) (Payne et al., 2015). In addition, the least significant difference between genotypes was estimated at the 5% significance level. The additive main effect and multiplicative interaction (AMMI) model (Gauch, 2006) was performed to assess patterns of stability for grain yield and days to heading. Other stability measures, ecovalence (Wricke, 1962) and the index of cultivar superiority of Lin and Binns (1988), were calculated as indicators of genotype-by-environment interaction.

3. Results

3.1. Climate conditions and barley vernalization

The potential for vernalization was evaluated at the three experimental sites by assessing changes in the number of cold nights (i.e. nights with a minimum temperature below 10C). This index was computed independently for each winter month (December, January, February and March) from 2013 to 2016. Results suggested a high number of cold nights in all months and at all meteorological sites

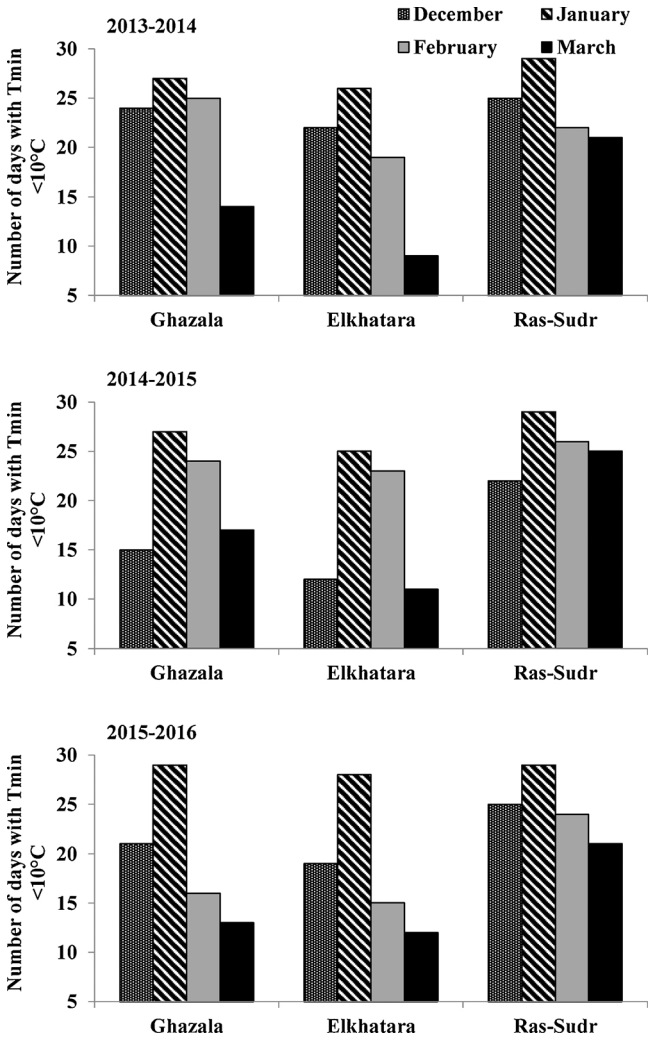

Fig. 2. Monthly frequency of cold nights, defined as days with minimum temperature lower than 10C during the extended winter (December–March) in three selected years.

(Fig. 2). However, the occurrence of cold nights was slightly higher during January compared to other months. Ras-Sudr showed a relatively higher number of cold nights relative to Ghazala and Elkhatara. In the majority of winter months and sites, minimum temperature during cold nights was in the range 6.5–9.4 °C, as depicted in Fig. S1. Taken together, our findings demonstrate a markedly high number of cold nights in all sites during wintertime and early spring, suggesting favourable climatic conditions for barley vernalization in Egyptian environments.

3.2. Genotypic differences with respect to growth habit genes

We detected unexpected genotypic differences in the vernalization genes in some local cultivars. In particular, two Egyptian cultivars, Giza

123 and Giza 126, were found to contain *Vrn-H1-4* and a dominant *Vrn-H2* allele, meaning that they are intermediate types similar to European genotypes Orria and Cierzo. In addition, the two strict winter genotypes, Barberousse and Hispanic, were verified as having a recessive *vrn-H1* and dominant *Vrn-H2*. Therefore, it was expected that they would require a considerable vernalization time to achieve timely induction of flowering, namely 6–8 weeks of cold temperatures. The remaining genotypes were classified as spring types, with dominant *Vrn-H1* alleles *(−2, −3)* and no vernalization requirements (Table 1). Regarding *HvCEN*, all local cultivars but one presented haplotype II (the fast one, according to Comadran et al., 2012), the same as European winter cultivars, and only one (Giza 127) had the haplotype III (the slow one), typical of European spring cultivars (Table 1). It is also noteworthy that almost all Egyptian cultivars contained the dominant allele at *Vrn-H2,* and the sensitive alleles at *Ppd-H1* and *Ppd-H2*, and the TC SNPs (the fast haplotype, according to Casas et al., 2011) at *Vrn-H3*. Therefore, this small set of Egyptian genotypes presented a genetic constitution at these major genes clearly veered towards earliness.

Another interesting finding is that, although the Egyptian cultivars are assumed to be of spring growth type, our results demonstrate that they belong to two distinct types, intermediate (Giza 123 and Giza 126) and spring (the remaining five cultivars). With regard to *HvCEN*, six Egyptian genotypes presented haplotype II, typical of European winter cultivars, whereas only one had the typical allele of spring cultivars. Therefore, there were spring and intermediate genotypes from both Egyptian and European origins in this study.

3.3. Genotypic performance in different environments

The analysis of variance revealed strong statistically significant differences among genotypes, locations and years for all studied traits (Table 4), albeit with a smaller effect of years compared to locations and genotypes. The location effect was larger than the genotypic effect for all traits, apart from days to heading, number of spikes per square meter and number of grains/spike. Significant interactions between genotypes, locations and years were detected for all traits. Interestingly, genotype-by-environment interaction for grain yield was dominated by genotype-by-location effects rather than genotype-by-year.

Mean yields were highest at Ghazala, intermediate at Elkhatara, and lowest at Ras-Sudr (Table S3). Causes of these differences could be the favorable soil conditions at Ghazala, which has higher water holding capacity than soils of other sites, and possibly more nutrients (Table S1). In particular, this type of soil has a slower drainage capacity and experiences less warming during springtime compared to sandy soils at Elkhatara and Ras-Sudr. These favourable conditions resulted in a better performance of cultivars throughout the growth cycle in Ghazala, as reflected in the higher grain yield and biomass, increased number of spikes per square-meter and larger thousand grain weight attained at this location compared to the other two locations (Tables S3, S5, S6, S7). On the other hand, the poor performance at Ras-Sudr is likely to be associated with salinity, which is prevalent in the region. All winter and intermediate genotypes, except for Barberousse, showed good performance in terms of grain yield under different environmental conditions (Tables 5 , S3). Pewter and Giza 126 produced the highest grain yield in all trials, ranging from 3538 (Giza 126 at RAS15) to 7966 (Pewter at Gh14) kg ha^{-1}. Similarly, Orria and Cierzo exhibited high values in all trials, with values ranging from 2508 (Orria at Sudr 16) to 7383 (Cierzo at Gh14) kg ha^{-1}.

With respect to days to heading, the overall mean values for the Egyptian cultivars showed a narrow span of 5 days (between 87 and 92 days after sowing). Overall, the European genotypes were clearly later (96–117 days; Table 5). Irrespective of these large differences in days to heading among the Egyptian and European cultivars, some of the foreign genotypes were as productive as the local ones, suggesting a potential of non-conventional germplasm in the Egyptian conditions. The latest genotype, Barberousse (winter), was clearly the least productive among all genotypes. It did reach heading and a moderate yield at all sites, indicating that this cultivar is probably out of its agroecological niche for good performance. In contrast, the performance of the other winter genotype (Hispanic) was very close to some of the Egyptian cultivars. This finding reveals the presence of ample variation for adaptation among winter cultivars, an interesting issue that deserves investigation in the future. In addition, Tardana showed a remarkable delay in flowering compared to other genotypes. The other five European genotypes reached heading between 96 and 99 days after sowing, which is about 7–10 days later than the local genotypes. However, grain yield did not appear to be affected by late flowering, except for Barberousse.

Generally, spring genotypes were earlier in heading and maturity than intermediate and winter ones (Tables 5, S3, S4). The two winter genotypes, Barberousse and Hispanic, showed very different heading patterns. While Barberousse was very late, Hispanic had similar days to heading to highly productive genotypes, such as Pewter (spring) and Cierzo and Orria (intermediate). Apparently, the two winter genotypes had very different earliness behavior. The earliest heading occurred at Ras-Sudr, mostly affected by the prevailing saline conditions.

Tables 5 and S5 indicate that the greatest above-ground dry matter in all studied environments occurred in some European genotypes, especially Tardana, Graphic and Pewter, compared to the Egyptian commercial cultivars. This feature may be a result of the longer growth cycle in the European cultivars. In contrast to other genotypes, Barberousse exhibited the lowest dry matter production in all environments.

Giza 128 and Pewter showed the highest number of spikes/m^2 in all trials (Tables 5, S6). In contrast, the lowest values were recorded for the Egyptian cultivars, Giza 2000, Giza 123 and Giza 133, with values

Table 4
Sums of squares of the joint ANOVA analyses for each trait recorded. The statistical significance was tested at a confidence level of 95% ($p < 0.05$).

Source of variance	df	PH†	DH	DM	GFP	NS/m^2	NGS	TGW	GY	AGDM
Genotype(G)	13	550.6**	1961.4**	1159.7**	179.1**	239530.8**	2133.9**	260.3**	10.39**	46.26**
Location (L)	2	4960.8**	9709.0**	42220.3**	12276.0**	860553.3**	1007.8**	2903.1**	343.63**	708.86**
Year (Y)	2	1522.1**	93.1**	11.7*	91.5**	17385.2**	177.3**	183.3**	5.97**	245.87**
GxL	26	56.0**	363.4**	110.6**	223.1**	15695.9**	27.5**	25.8**	1.79**	6.82**
GxY	26	107.4**	13.3**	18.4**	16.6**	4766.3**	25.7**	34.2**	0.84**	4.08**
LxY	3	168.7**	413.1**	365.5**	274.5**	3847.6**	51.2**	214.5**	4.00**	16.61**
GxLxY	39	33.4**	23.4**	27.6**	28.7**	4768.2**	13.0**	13.5**	0.68**	5.69**
Residual	222	43.6	4.9	3.3	7.8	43.6	1.1	2.1	0.06	0.37
Total	335	16743.6	173.6	315.9	110.4	16743.6	96.7	38.1	2.85	9.40

* p-value < 0.05.

** p-value < 0.01, df (degrees of freedom).

† PH: plant height (cm), DH: days to heading, DM: days to maturity, GFP: grain filling period, NS/m^2: number of spikes per square meter, NGS: number of grains per spike, TGW: thousand-grain weight (g), GY: grain yield (ton/ha) and AGDM: above-ground dry matter (ton/ha).

Table 5
Overall genotypic mean values for each measured trait, across all field trials.

Genotypes	PH†	DH	DM	GFP	NS/m^2	GNS	TGW	GY	AGDM
Giza 123	80.0	87.0	122.5	35.6	303	42.5	45.16	5316	16793
Giza 126	81.6	87.1	124.2	37.2	296	47.2	47.69	5864	16419
Giza 127	77.1	90.4	124.9	34.5	503	24.2	47.71	5232	15514
Giza 128	75.2	89.3	126.1	36.8	501	22.0	44.55	4702	14976
Giza 2000	79.8	88.2	126.3	38.2	272	40.3	46.76	4587	15419
Giza 132	78.0	86.8	125.0	38.2	256	44.7	44.87	4381	14544
Giza 133	79.0	91.9	125.1	33.2	260	43.5	47.1	4867	16599
Barberousse	71.8	117.0	145.0	28.1	296	37.3	36.12	3424	14081
Cierzo	74.4	96.9	131.5	34.6	330	43.5	43.63	5527	14617
Graphic	70.1	96.1	129.7	33.7	474	26.2	41.79	4924	18316
Hispanic	66.3	98.6	132.0	33.4	442	23.6	43.98	4150	16587
Orria	71.6	97.1	129.0	31.9	311	42.6	43.53	5302	16695
Pewter	67.5	98.6	131.1	32.5	518	24.3	47.35	5692	17322
Tardana	75.5	110.5	144.2	33.7	319	39.9	39.91	4611	18661
Average	**74.9**	**95.4**	**129.8**	**34.4**	**363**	**35.8**	**44.30**	**4898**	**16182**

† PH: plant height (cm), DH: days to heading, DM: days to maturity, GFP: grain filling period, NS/m^2: number of spikes per square meter, NGS: number of grains per spike, TGW: thousand-grain weight (g), GY: grain yield (kg ha^{-1}) and AGDM:above-ground dry matter (kg ha^{-1}).

ranging between 147 and 294 spikes/m^2. In comparison, winter and intermediate European genotypes showed intermediate and high values in all trials, varying from 180 (Tardana at Sudr16) to 615 spikes/m^2 (Pewter at Gh14).

The lower number of spikes in the Egyptian cultivars was compensated for by a large number of grains/spike, at least for the six-rowed ones (Giza 126, Giza 132 and Giza 133). Overall, the European genotypes showed lower values than local genotypes in all trials (Tables 5, S6). Overall, the lowest number of grains/spike was found in Giza 127, Giza 128 and Hispanic (all two-rowed genotypes).

The highest thousand-grain weight occurred in Pewter, Giza 126, Giza 127 and Giza 2000 in all trials, with values ranging from 39.31 (Giza 2000 at Sudr16) to 58.83 g (Giza 127 at GH 16) (Tables 5, S7). Other genotypes, Orria, Cierzo and Hispanic, presented intermediate values, ranging from 35.90 g (Orria at Sudr16) to 51.15 g (Orria at Gh16). These results reveal significant differences among locations in terms of thousand-grain weight, as well as duration of the grain filling period. For these two traits, the largest values were obtained at Ghazala, while the lowest values were recorded at Ras-Sudr (Table S4, S7).

3.4. Genotype-by-environment interactions

The genotype-by-environment interaction for grain yield was dominated by the influence of winter cultivars. Barberousse and Hispanic presented the highest ecovalence (Table 6) and were also clearly the most distant from the origin in the AMMI biplot (Fig. 3). The intermediate genotypes, except Tardana, showed ecovalence values not larger and, in some cases, were even smaller than in spring genotypes,

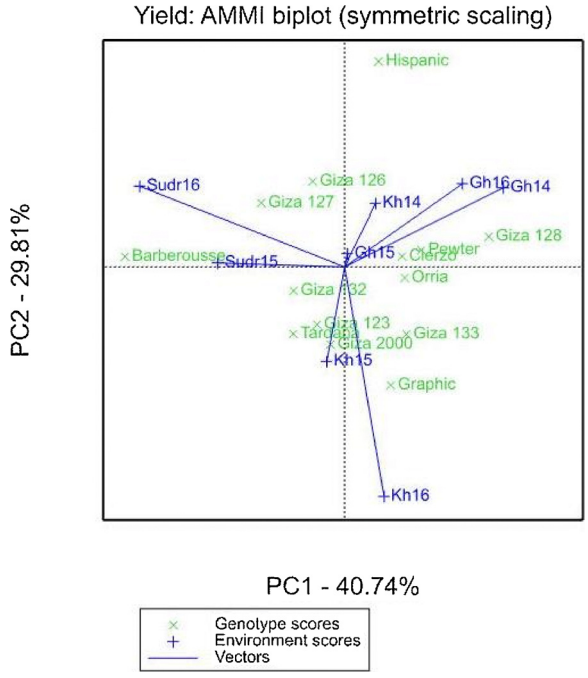

Fig. 3. Biplot summarizing the first two principal components resulting from the AMMI analysis of grain yield.

Table 6
Genotypic averages and stability indices.

Genotypes	Growth type	Yield (kg ha^{-1})	Cultivar superiority (CS)	CS ranking	Ecovalence	Ecovalence ranking
Giza 123	Intermediate	5316	468645	5	1922949	9
Giza 126	Intermediate	5864	49981	1	1595788	8
Giza 127	Spring	5232	512742	6	2032988	10
Giza 128	Spring	4702	1236536	10	3935490	12
Giza 2000	Spring	4587	1221885	9	1486214	4
Giza 132	Spring	4381	1496050	12	1546351	6
Giza 133	Spring	4867	878804	8	1542560	5
Barberousse	Winter	3424	3866662	14	6661224	14
Cierzo	Intermediate	5527	225252	3	474327	1
Graphic	Spring	4924	844115	7	2478475	11
Hispanic	Winter	4150	2086422	13	4993739	13
Orria	Intermediate	5302	389163	4	558965	2
Pewter	Spring	5692	143443	2	894744	3
Tardana	Intermediate	4611	1254416	11	1550412	7

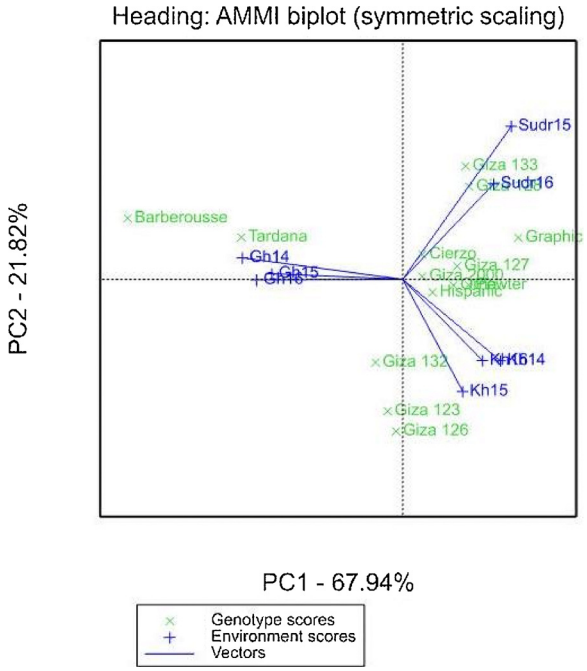

Fig. 4. Biplot summarizing the first two principal components resulting from the AMMI analysis of days to heading.

and clustered close to the origin in the AMMI biplot (Fig. 3). This clearly indicates that they are at least as stable as spring cultivars. With regard to days to heading, roughly 90% of the genotype-by-environment interaction was summarized by only two principal components (Fig. 4). These first two axes showed a clear geographic prevalence of the G × E interaction. In particular, it presents some relatively later genotypes at Ghazala (Barberousse and Tardana), Elkhatara (Giza123, Giza126) and Ras-Sudr (Giza133, Giza128). These differences cannot only be seen in the context of vernalization potential, as the differences in the number of nights with low minimum temperatures were lower at Ghazala and Elkhatara, though being slightly higher at Ghazala. This finding clearly suggests that it is important to consider other climatic and environmental factors to explain the late behavior of Barberousse and Tardana at this location.

The correlation coefficients among traits in the eight field trials indicated the presence of slightly different patterns among the locations (Table S8).

4. Discussion

Climate change poses a great challenge to agricultural production all over the world (De la Casa and Ovando, 2014). Egypt is one of the developing countries which is highly exposed to climate change with increasing threats to food security (El Kenawy et al., 2009; El Shaer and Al Dakheel, 2017). Within this context, this study endeavors to evaluate the performance of winter and intermediate barley genotypes under Egyptian field conditions, with the aim of identifying other possible patterns of adaptation beyond the well-known strictly spring cultivars. Indeed, adaptation of cereals to climate change through more resilient crops is in highly demand, particularly in arid environments such as Egypt (Dwivedi et al., 2017; Ingvordsen et al., 2015; Kole et al., 2015; Veenstra et al., 2017). The projected climate changes under different scenarios of greenhouse gas emission could induce changes in the frequency, intensity and duration of extreme weather thermal conditions, with drastic impacts on winter cereal crops (Lv et al., 2013). Currently, there is a trend to go back to landraces in search of adaptation traits to improve yields for stressful conditions (Newton et al., 2010). However, local varieties and landraces per se, at least in Mediterranean conditions, are only competitive below rather low yield thresholds (Pswarayi et al., 2008; Yahiaoui et al., 2014). New genetic combinations with increased adaptation could be developed by hybridization between foreign and local varieties to obtain genotypes that could perform better under anomalous low winter temperatures specific to the Egyptian continental climate.

It is remarkable that, for most traits, the largest interaction factor involving genotypes was *genotype* × *location* (G × L), indicating a dominant geographic factor in the interaction. The distinctiveness of the saline environment of Ras-Sudr has already been pointed out, as well as the superior water holding capacity of Ghazala. In fact, grain yield showed a clear positive correlation with the duration of the grain-filling period only at Ghazala (Table S8), whereas in the other two locations this correlation was weaker or even negative. This indicates better conditions at Ghazala during grain filling, also suggested by the larger correlation coefficients of thousand-grain weight with grain yield at Ghazala.

Our results indicate that the range of optimum flowering dates was larger than the narrow window displayed by the local genotypes. For instance, the UK-bred cultivar Pewter, which is on average one week later than the Egyptian cultivars, showed good adaptation to the Egyptian environment, with the second highest yield average among all genotypes. Also, the intermediate genotypes showed a generally similar performance to the spring ones.

Intermediate genotypes were the most abundant group in barley landraces from southern Spain (Casao et al., 2011b), indicating specific adaptation to the warm Mediterranean winters. They are characterized by having a winter allele at *Vrn-H2,* combined with allele *Vrn-H1-4*, an active allele at *Ppd-H2* and a sensitive allele at *Ppd-H1*. This combination is uncommon in winter cultivars from northern latitudes (Casao et al., 2011b; Hemming et al., 2009; Szűcs et al., 2007). The two Egyptian cultivars found with this haplotype for those four genes were among the best performers in this experiment (ranked first and fourth for grain yield), with low genotype-by-environment interaction and good stability. It could be speculated that these commonalities of adaptation haplotypes and growth habit between the Egyptian cultivars and the Spanish landraces could be traced to common ancestry dating back to the Neolithic expansion of the crop through the Mediterranean basin. This syndrome of adaptation has only recently been documented and has neither been consciously exploited in breeding nor thoroughly tested. This study confirms the potential of the supposedly adapted germplasm, such as the European spring genotypes (e.g. Pewter) and intermediate genotypes (e.g. Cierzo, Orria, Giza123 and Giza 126), for breeding for autumn sowings in Egypt. Importantly, this finding might be applicable to other regions with warmer winters which are not limited to the Mediterranean basin. Indeed, Rodriguez et al. (2008) reached a similar conclusion, stating that improved genotypes incorporating adaptation from landraces tolerated erratically variable conditions better than other varieties and landraces themselves.

Some intermediate European genotypes (e.g. Cierzo and Orria) presented desirable high values for the number of grains/spike, grain weight and grain and straw yield, compared to local commercial cultivars. Though not specifically tested in this experiment, these genotypes are a potential source of cold tolerance for any unfavorable climate change. In fact, the population from which Cierzo originated showed the most important grain yield QTL at *Vrn-H1* (Igartua et al., 2015; Mansour et al., 2014) in field trials carried out in Spain, with *Vrn-H1-4* as the favourable allele (in contrast with a winter allele). As such, they could be introduced in barley breeding programs for releasing new adapted genotypes which are resilient to climate change. The potential for improving yields in Mediterranean environments by modifying *Vrn-H1* allele with exotic material has been previously demonstrated by Rollins et al. (2013), by using Australian spring cultivar Keel as donor.

It was remarkable that all introduced winter and intermediate genotypes reached flowering, indicating that the accumulation of low temperature under the Egyptian climatic condition meets the

vernalization requirements of these genotypes. Nonetheless, the cold period was insufficient to meet the requirements of a more strict winter barley (such as Barberousse) in order to achieve high yield. Recalling that the three selected experimental sites are located in northern Egypt, it is expected that these genotypes will be induced for flowering even more in southern Egypt, because southern Egypt has a more continental climate and, thus, colder winters than in northern Egypt (El Kenawy et al., 2010, 2016).

It is noticeable that a winter genotype, such as Hispanic, flowered as early as some intermediate and spring genotypes. Even its yield level, though low, was not disimilar to the spring genotypes. Although it cannot be inferred that this genotype was adapted to the conditions of these experiments, it performed unexpectedly well for a winter genotype. Hispanic has a similar vernalization requirement to Barberousse (E. Igartua, unpublished), but the effect of *Ppd-H2* on hastening development under short days seems to be fully exploited in the Egyptian conditions. Hispanic has been one of the most successful cultivars in Spain for the last 20 years. According to the official data of the Spanish Ministry of Agriculture, Fisheries, Food and Environment (MAPAMA, 2017), it has consistently been among the top three cultivars for sales of certified seed since 2009. It presents the active allele at *Ppd-H2*, providing extra earliness and a complement for vernalization when this is not complete (Casao et al., 2011b). Taken together, it can be seen that the genetic features of this cultivar facilitate its adaptation to a wide spectrum of environmental conditions, being a resilient cultivar. This message should be of interest to breeders seeking adaptations to climate change conditions in Egypt and other countries with similar climatic conditions.

5. Conclusions

This study presents the first attempt to assess the agronomic value of different growth habits of barley in the Egyptian environment. A particular focus is the evaluation of whether vernalization requirements in barley can be impacted significantly by recent climate change and variability over Egypt. Results demonstrate that, under the current climate conditions, both winter and intermediate barley genotypes revealed their potential in the exploration of alternative patterns of adaptation. In addition, this study offers the possibility to widen the available genetic base for breeding by displaying the potential of yet unexploited genotypes with good adaptation for increased yield and stability. Consequently, genetic variability could be exploited by crossing these genotypes with commercial cultivars, with the aim of realizing genotypes that could perform better under limited vernalization requirements, which can be fulfilled in the Egyptian environment.

It was assumed that all commercial barley cultivars in Egypt have a strict spring growth habit. Nonetheless, this study suggests that there are, at least, two currently used cultivars (Giza 123 and Giza 126) which are intermediate genotypes with likely limited vernalization requirements. These genotypes could be advantageous in breeding in regions with warmer winters, which are common in the Mediterranean basin.

This study indicates that the range of optimum heading date is larger than the narrow range exhibited by the commercial cultivars. This finding was evident for cultivar Pewter, which was later than the latest Egyptian cultivars and exhibited higher grain yield and aboveground dry matter production, representing good adaptation. Overall, these findings demonstrate the potential of non-conventional germplasm to face the future challenges of climate change in Egypt and possibly in other Mediterranean countries.

Acknowledgements

We are grateful to the Egyptian Meteorological Society for providing the climatic data used in this study. AMC and EI acknowledge funding from Spanish MINECO, grants AGL2013-48756-R and AGL2016-80967-R.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.fcr.2018.04.016.

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